BIOLOGIA PLANTARUM 34 (3-4): 241-251, 1992

Influence of reproductive organs on plant senescence in rice and wheat

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Abstract

The chlorophyll and protein contents of the flag, second and third leaves gradually decreased during the reproductive development of rice (*Oryza sativa* L. cv. Rasi) and wheat (*Triticum aestivum* L. cv. Sonalika) plants, whereas proline accumulation increased up to the grain maturation stage and slightly decreased thereafter. In rice plant, the rate of decrease in chlorophyll and protein and increase in proline level were higher in the flag leaf than in the second leaf. It was opposite in wheat plant. The export of [^{32}P]-phosphate from leaves to grains gradually increased reaching a maximal stage at the grain development stage, and then declined. The export of this radioisotope was greater in rice than in wheat. Removal of panicle at the anthesis and grainfilling stages delayed leaf senescence of rice plant, while in wheat the ponicle removal at any stage did not have a marked effect on delaying leaf senescence. The contents of chlorophyll and protein of glumes were higher in wheat than in rice. The variation of such source-sink relationship might be one of the possible reasons for the above effect on leaf senescence.

Introduction

The developing seeds are the predominant metabolic sink following anthesis which influences different metabolic activities related to senescence. Thus, the presence of reproductive sink stimulates the photosynthetic activity of the leaves, and photosynthates are rapidly translocated to the grains (Rawson *et al.* 1976, Nooden and Guiamet 1989). The removal of reproductive sink has different effects on leaf senescence, such as the delaying or acceleration, or sometimes it is without effect. The effectiveness of such treatment was related to the time of removal (Patterson and Brun 1980). Leopold *et al.* (1959) suggested that removal

Received 25 April 1991, *accepted* 7 August 1991.

Acknowledgement: The authors acknowledge the financial assistance rendered by the Council of Scientific and Industrial Research in the form of a Junior Research Fellowship to R.I. Khan.

of flowers, young pods or ripening fruits from soybean plant delayed leaf yellowing. Removal of flowers or fruits delayed leaf senescence in wheat (Patterson and Brun 1980, Biswas and Mondal 1986), rice (Ray and Choudhuri 1981, Mondal and Choudhuri 1984 and soybean (Wittenbach 1983), while such treatment in maize (Allison and Weinmann 1970) and *Capsicum annuum* (Hale and Brady 1977) hastened senescence. On the other hand, such treatment on *Xanthium pensylvanicum* showed no effect (Krizek *et al.* 1966). Thomas and Stoddart (1980) have stated that removal of sink hastems the induction of senescence process where growth of the sink mainly depends on the current photosynthesis. The sterile glumes have also some role in the grain-filling process (Thorne *et al.* 1968) and the extent of such involvement varies amongst cultivars (Saghir *et al.* 1968, Khanna-Chopra and Sinha 1981). The relationship of senescence with source-sink activity thus variable in different species and even cultivars. The whole plant senescence is a genetically programmed process that can be modified by external factors (Thomas and Stoddart 1980). Mainly two hypotheses are competing with each other for the mechanism of monocarpic or whole plant senescence. The senescence factor hypothesis (Lindoo and Nooden 1977, Nooden 1988) suggests that a senescence factor probably hormonal in nature originates in the seeds, migrates to the rest of the plant and induces the senescence process. Another, the nutrient withdrawal hypothesis (Molisch 1938, Ray and Choudhuri 1981, Mondal and Choudhuri 1984, Biswas and Mondal 1986, Hamilton and Davies 1988, Kelly and Davies 1988, Engvild 1989) takes the mobilization of metabolites from vegetative to reproductive parts for the main cause of senescence. But the actual triggering mechanism of monocarpic senescence is still for from being clear. The present study investigated the role of reproductive structures on whole plant senescence of rice and wheat and the possible mechanism of monocarpic senescence.

Materials and methods

Healthy and viable seeds of rice (*Oryza sativa* L. cv. Rasi) and wheat (*Triticum aestivum* L. cv. Sonalika) were procured from the Crop Research Farm of Burdwan University. Seeds were surface-sterilized in 0.1 % (m/v) mercuric chloride ($HgCl_2$) for 1 min, followed by washing several times in tap water. Seeds then germinated at 37 °C in trays with a moistened blotting paper, and they were grown in earthen pots (high 25 cm, diameter 30 cm), where cowdung was used as the only manure. Five sets of each rice and wheat plants (15 pots per set) were used for experiments: One set of plants with intact panicle served as control, while in the remaining four sets the panicle was removed at different reproductive stages, *i.e.* anthesis (day 0), grain-filling (day 7 after anthesis), grain development (day 14), and grain maturation (day 21). The duration of reproductive phase in both plant species was more or less the same.

The flag, second and third leaves and glumes of control plants and only the leaves of surgically altered plants were collected in rice and wheat, respectively, at different reproductive stages, *i.e.* grain-filling (105, 65 d), grain development (112, 72 d), grain maturation (119, 79 d) and senescence (126, 86 d), and chlorophyll, protein and proline contents were measured.

Chlorophyll amount was estimated from the samples according to Arnon's (1949) method. For protein estimation, samples were homogenised with 80 % ethanol and made phenol-free by washing successively with cold 10 % trichloroacetic acid, ethanol, ethanol : chloroform (3:1), ethanol : ether (3:1), and finally with ether according to Kar and Mishra (1976). The protein content was estimated according to Lowry *et al.* (1951). Proline was extracted by 3 % sulfosalicylic acid and estimated according to Bates *et al.* (1973).

To analyse the role of reproductive structures on mobilization of metabolites from leaves to grains as well as senescence, the export of [^{32}P]-phosphate from leaves to grains was recorded. The [^{32}P]-phosphate was fed separately through the tips of flag, second and third leaf of control plants for 24 h with 1 cm^3 of radiophosphate as $H_3{}^{32}PO_4$ (19.9 MBq) in 0.1 M sodium citrate buffer at pH 6.5. The radiophosphate translocation to the seeds was measured with a Geiger-Muller counter (*cf.* Mondal and Choudhuri 1985 for details).

Each experiment was repeated thrice with three replicates in each set. The data were statistically analysed for LSD at $P = 0.05$ (Panse and Sukhatme 1967) at the treatment and replication levels.

Results and discussion

The chlorophyll and protein contents of the flag, second and third leaf of control rice and wheat plants gradually decreased during the reproductive development, whereas proline accumulation increased up to grain maturation and then slightly decreased (Tables 1-3). In rice the rate of decline of both chlorophyll and protein was faster in the flag leaf than in the second leaf, while this was just reverse in wheat (for chlorophyll changes during leaf development of various plant species see •esták 1977). Also, the proline accumulation in rice plant was greater in the flag leaf than in the second leaf up to the grain maturation stage but this was just opposite in wheat (Table 3). Hence, rice and wheat plants showed nonsequential and sequential pattern of leaf senescence (Mondal and Choudhuri 1984, Biswas and Mondal 1986), respectively.

The export of [^{32}P]-phosphate to the grains was significantly greater from the flag leaf than from the second and third leaves in both the rice and wheat cultivars, which reached a maximal point at the grain development stage (day 14) and declined the reafter (Fig. 1). Thus the maximal grain-filling took place within 14 d after anthesis and flag leaf was the main exporter of photosynthates to the grains,

Table 1. Effect of panicle removal at different reproductive stages on changes in chlorophyll (Chl) and protein contents [g kg^{-1}(fr.m.)] in the flag, second and third leaf of rice (cv. Rasi) during reproductive development. (DAA - days after anthesis). Figures within parentheses indicate percentage increase (+) or decrease (-) against control.

Treatment: Panicle removed at DAA	Leaf position	Time after anthesis [d] 7		14		21		28	
		Chl	Proteins	Chl	Proteins	Chl	Proteins	Chl	Proteins
Control	flag	1.22	71.0	0.79	60.0	0.34	49.0	0.12	37.0
	second	0.96	62.0	0.71	56.0	0.36	46.0	0.20	44.0
	third	0.72	58.5	0.52	50.0	0.16	40.5	0.04	33.8
0*	flag	1.16(-4.9)	72.0(+1.4)	0.93(+18)	62.0(+3.3)	0.43(+26)	58.2(+16)	0.27(+125)	48.5(+31)
	second	0.98(+2.0)	63.4(+2.2)	0.74(+5)	58.0(+3.4)	0.46(+27)	54.5(+17)	0.26(+30)	47.0(+6.8)
	third	0.73(+2.7)	60.5(+3.4)	0.54(+3)	52.2(+4.0)	0.19(+18)	44.5(+10)	0.08(+100)	38.4(+12)
7**	flag	-	-	0.78(+1.2)	60.5(+0.8)	0.42(+23)	55.5(+12)	0.25(+108)	47.5(+28)
	second	-	-	0.73(+2.8)	60.6(+8.2)	0.44(+22)	51.0(+12)	0.24(+20)	47.0(+6.8)
	third	-	-	0.53(+2.0)	52.3(+4.6)	0.19(+18)	45.3(+12)	0.07(+75)	37.0(+9.4)
14+	flag	-	-	-	-	0.35(+2.9)	50.2(+2.0)	0.13(+8.3)	38.0(+2.8)
	second	-	-	-	-	0.36(±0)	47.2(+2.5)	0.20(±0)	41.5(-5.6)
	third	-	-	-	-	0.15(-6.0)	40.0(-2.8)	0.05(+25)	34.4(+3.8)
21++	flag	-	-	-	-	-	-	0.14(+13)	38.0(+2.6)
	second	-	-	-	-	-	-	0.19(-8.4)	45.0(+2.4)
	third	-	-	-	-	-	-	0.03(-25)	34.0(+1.6)
LSD at P=0.05		0.0082	0.86	0.0039	1.2	0.0046	1.54	0.0094	1.33

Stages of grain development: * - anthesis, ** - grain filling, + - grain development, ++ - grain maturation

Table 2. Effect of panicle removal at different reproductive stages on changes in chlorophyll (Chl) and protein contents [g kg^{-1}(fr.m.)] in the flag, second and third leaf of wheat (cv. Sonalika) during reproductive development. (DAA - days after anthesis). Figures within parentheses indicate percentage increase (+) or decrease (-) against control.

Treatment: Panicle removed at DAA	Leaf position	Time after anthesis [d] 7		14		21		28	
		Chl	Proteins	Chl	Proteins	Chl	Proteins	Chl	Proteins
Control	flag	1.01	68.0	0.74	56.0	0.53	48.0	0.20	39.0
	second	0.92	61.0	0.63	51.0	0.44	43.0	0.12	34.0
	third	0.74	54.0	0.51	47.0	0.21	39.0	0.04	30.0
0*	flag	1.09(+8.1)	72.2(+6.1)	0.76(+2.7)	58.0(+3.5)	0.59(+11.3)	52.0(+8.4)	0.26(+30)	44.0(+12)
	second	0.93(+1.0)	63.0(+3.2)	0.65(+3.1)	54.0(+5.8)	0.47(+6.8)	48.0(+11.6)	0.19(+36)	37.8(+11)
	third	0.76(+2.7)	54.5(+1.2)	0.53(+4.0)	50.0(+5.4)	0.26(+23)	41.1(+5.3)	0.06(+50)	33.5(+11)
7**	flag	-	-	0.73(-1.3)	57.0(+1.8)	0.56(+5.6)	49.5(+2.4)	0.22(+10)	41.0(+7.6)
	second	-	-	0.64(+1.5)	54.0(+5.8)	0.43(+2.3)	44.0(+2.6)	0.14(+16)	35.5(+4.4)
	third	-	-	0.52(+2.0)	46.5(-1.0)	0.24(+8.5)	40.5(+3.6)	0.046(+15)	31.6(+5.3)
14+	flag	-	-	-	-	0.53(±0)	49.0(+2.2)	0.21(+5)	40.0(+2..5)
	second	-	-	-	-	0.45(+2.3)	42.6(-1.6)	0.11(+8)	33.6(-1.6)
	third	-	-	-	-	0.23(+8.6)	38.5(-1.8)	0.05(+25)	31.0(+3.1)
21++	flag	-	-	-	-	-	-	0.20(±0)	40.0(+2.6)
	second	-	-	-	-	-	-	0.13(+8)	33.0(-3.4)
	third	-	-	-	-	-	-	0.04(±0)	30.5(+1.6)
LSD at P=0.05		0.0033	0.62	0.0041	0.94	0.0068	1.20	0.0051	1.06

Stages of grain development: * - anthesis, ** - grain filling, + - grain development, ++ - grain maturation

Table 3. Effect of panicle removal at different reproductive stages on changes in proline content [mg kg^{-1}(fr.m.)] in the flag, second and third leaf of rice and wheat during reproductive development. (DAA - days after anthesis). Figures within parentheses indicate percentage increase (+) or decrease (-) against control.

Panicle removed at DAA	Leaf position	Time after anthesis [d] 7		14		21		28	
		Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat
Control	flag	4.2	4.4	5.6	5.2	7.3	6.7	6.0	6.4
	second	4.6	4.8	5.8	5.6	7.0	6.8	6.3	5.6
	third	5.8	6.0	7.2	5.9	7.0	6.7	5.4	4.0
0*	flag	4.5(+7.1)	4.0(-9.0)	5.1(-8.9)	4.8(-7.6)	6.2(-15.0)	5.9(-11.9)	6.8(-10.0)	6.3(-1.5)
	second	4.8(+4.3)	5.0(+4.1)	5.4(-3.5)	5.4(-3.5)	6.0(-14.5)	6.1(-10.0)	6.5(+8.1)	5.8(+3.5)
	third	5.9(+1.7)	6.2(+3.3)	6.3(-12.5)	6.4(-7.2)	6.3(-7.4)	6.2(+3.7)	5.6(+3.7)	4.4(+10.0)
7**	flag	-	-	5.8(+3.5)	5.5(+5.7)	5.9(-19.0)	6.2(-7.4)	6.4(+6.6)	6.3(+1.5)
	second	-	-	5.4(-6.8)	5.4(-3.5)	6.2(+11.4)	6.4(-5.8)	6.5(+3.1)	5.2(-8.5)
	third	-	-	6.8(-5.5)	6.1(+2.3)	6.0(+14.0)	6.2(-7.4)	5.8(+7.4)	4.4(+10.0)
14+	flag	-	-	-	6.9(-5.4)	6.9(-5.4)	6.5(+2.9)	6.1(+1.6)	5.6(+1.4)
	second	-	-	-	7.1(+1.4)	7.1(-1.4)	6.7(-1.4)	6.4(+1.5)	5.6(±0)
	third	-	-	-	7.2(+2.8)	7.2(-2.8)	6.5(-3.1)	5.3(+1.8)	4.1(+2.5)
21++	flag	-	-	-	-	-	-	6.2(+3.3)	6.3(-1.5)
	second	-	-	-	-	-	-	6.4(+1.5)	5.7(-1.7)
	third	-	-	-	-	-	-	5.2(+3.7)	4.1(+2.5)
LSD at P=0.05		0.13	0.22	0.34	0.31	0.16	0.26	0.22	0.19

Stages of grain development: * - anthesis, ** - grain filling, + - grain development, ++ - grain maturation

perhaps due to its greater proximity to the sink. Though the seed mass in rice and wheat plants was more or less equal (data not shown), the export of radioisotope from leaves to grains was significantly greater in rice than in wheat, which can be further substantiated from the availability of photosynthates from the reproductive structures for grain- filling. The flag leaf of rice underwent greatest nutrient deprivational stress at the grain development stage and registered the earliest senescence syndrome, whereas in wheat both the flag and the second leaf equally participated in the progress of nutrient export and the second leaf (older than the flag leaf) senesced earlier than the flag leaf.

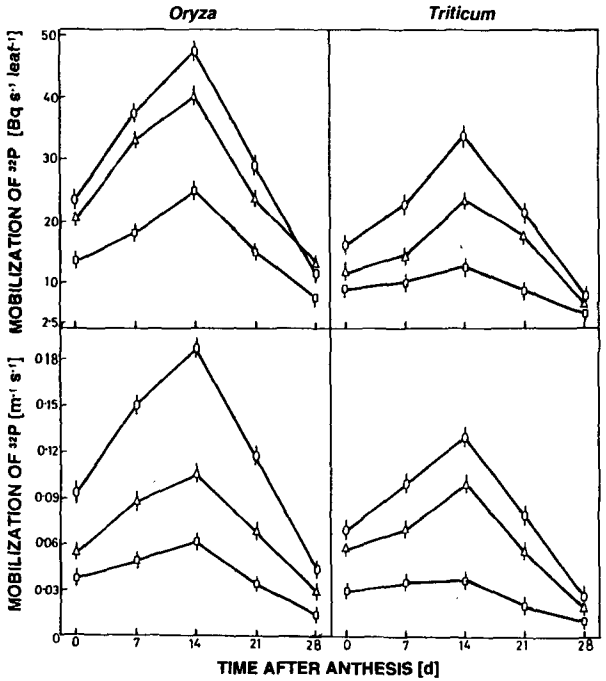

Fig. 1. Changes in the export of [^{32}P]-phosphate from the flag (*circles*), second (*triangles*) and third (*squeres*) leaf to the grains during the progress of reproductive development.

The accumulation of proline senescence has been reported in isolated (Wang *et al.* 1982) and intact (Stewart 1980, Mondal *et al.* 1984) leaves. The present experiments with rice and wheat plants showed similar results (Table 3) and we know that proline accumulation is a reliable indicator of stress development. Thus the mobilization of metabolites from leaves to grains caused a nutrient deprivational stress in the source organ (Biswas and Choudhuri 1980). The nutrient deprivational stress, thus imposed, possibly led to an increase in the ratio of abscisic acid to cytokinins (Ray and Choudhuri 1981). Such stress induced

ABA accumulation, in turn, enhances proline accumulation in plants (Hsiao 1973, Aspinall 1980). The exact role of proline in a senescing plant is not clear: like ABA, proline can promote stomatal closure (Rajagopal 1981, Raghavendra and Reddy 1988). Stomatal closure causes drastic reduction of transpiration and eventual translocation of cytokinins from roots (Itai and Vaadia 1971) which may favour senescence of the whole plant.

The removal of panicle at the anthesis (day 0) and grain-filling stage (day 7) of rice plant reduced the loss of chlorophyll and protein up to the senescent stage (Table 1) and proline accumulation up to the grain maturation stage (Table 3) over the untreated control plants and delayed leaf senescence. Such treatment also modified the pattern of leaf senescence from the nonsequential to the sequential mode in rice. The removal of panicle after grain-filling stage had no effect. Similarly, such treatment on wheat plant at anthesis and grain-filling stage slightly delayed senescence but the delaying effect was significantly lower than that observed in rice plant (Table 2). Panicle removal after the grain-filling stage had no effect on leaf senescence; an eventual effect of panicle removal on delaying leaf senescence may be species or cultivar specific (Crafts-Brandner *et al.* 1984).

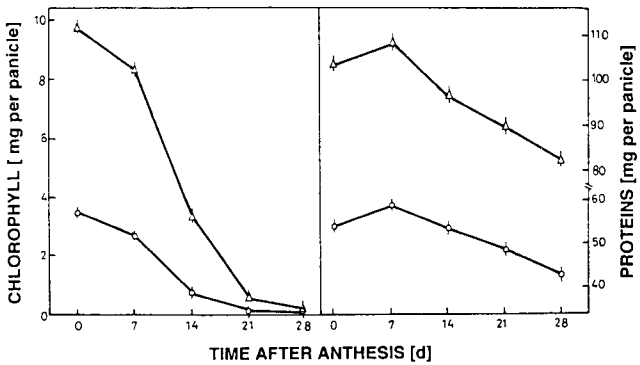

Fig. 2. Changes in the total chlorophyll and protein contents in the glumes of a panicle of rice (*circles*) and wheat (*triangles*) during the progress of reproductive development.

Another reason of such difference may be ascribed to the greater availability of current photosynthate produced by the glumes and awns in wheat than in rice (Evans and Rawson 1970, Blum 1985): the glumes and awns are important sources for the supply of assimilates to grains (Thorne 1965, Thorne *et al.* 1968, Saghir *et al.* 1968). Biswas and Mondal (1986) suggest that wheat glumes act as intermediaries in the transfer of photosynthates from leaves to grains and the contribution of flag leaf is rather indirect. According to Khanna-Chopra and Sinha (1981) the relative photosynthetic capacity of ears in wheat is several times higher than that of the flag leaf on unit chlorophyll basis. Saghir *et al.* (1968) have also

found that exposed ear parts of wheat, such as glumes and awns, supply 60 % or more assimilates for grain-filling. The evidence in favour of this explanation may be provided from the results of chlorophyll and protein contents of the glumes (Fig. 2), which showed that the initial content of both chlorophyll and protein in glumes was significantly higher in wheat than in rice, but the decline of these components was much greater in wheat than in rice during reproductive development. Thus the contribution to grain-filling from the leaves of rice was greater than that of wheat (Murata and Matsushima 1975). Conversely, the contribution of ear photosynthesis to grain-filling is far less pronounced in rice than in wheat (Thorne 1965). This was also supported by the data that the export of [^{32}P]-phosphate from the leaves to the grains was significantly less in wheat than in rice. Such difference in export may be one of the possible reasons of the differential effects of panicle removal on senescence in these two plants. Removal of panicle or sink only delayed senescence for a certain time but it could not prevent the whole plant senescence. Thus, the nutrient export from source to sink may be the actual triggerer of senescence, but it enhances the senescence which is already switched on, perhaps during flowering, because senescence of photoperiod-sensitive plants can be prevented for almost an indefinite period by inhibiting flowering by subjecting them to unfavourable conditions (Osborne 1985, Choudhuri and Mondal 1988). Hamilton and Davies (1988) have suggested that during flowering nutrient partitioning took place and all the assimilates are exported to the reproductive parts depriving rest of the plant parts, thereby inducing whole plant senescence. Thus nutrient withdrawal is the prime factor for accelerating senescence (Molisch 1938, Mondal and Choudhuri 1984, Kelly and Davies 1988) which is switched on presumably during flowering initiation. The exact biochemical mechanism of switching on of senescence inducing genes during floral differentiation however remains to be understood.

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